HILGARDIA

A JOURNAL OF AGRICULTURAL SCIENCE

PUBLISHED BY THE

CALIFORNIA AGRICULTURAL EXPERIMENT STATION

VOL. 4 NOVEMBER, 1929 No. 7

FACTORS WHICH MODIFY THE RESISTANCE OF WHEAT TO BUNT, TILLETIA TRITICI[1, 2]

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In an earlier publication[(2)] [4] the author presented data which indicated that Martin wheat differs from such susceptible varieties of wheat as White Federation and Hard Federation in one main dominant factor for resistance to bunt, *Tilletia tritici*, and that Hussar wheat differs from these susceptible varieties in two main factors for resistance, one of which was shown to be identical with the Martin factor.

Because some susceptible plants nearly always escape infection it was necessary to classify F_2 on the basis of percentages of bunt in F_3 rows which were grown from the seed of individual F_2 plants. Although Martin and Hussar were completely free from bunted plants, there were not enough bunt-free F_3 rows to make up the resistant classes. A few rows with a low percentage of bunt had to be included in the resistant groups. At that time it was pointed out that the presence of a few diseased plants in resistant rows might be due to modifying factors. Also it was suggested that genetically resistant plants occasionally might become infected. Data now are available

[1] Cooperative Investigations of the Office of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture, and the Division of Agronomy, California Agricultural Experiment Station.

[2] The writer acknowledges valuable suggestions from Dr. R. E. Clausen, Division of Genetics, University of California, and various members of the Office of Cereal Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture.

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[4] Superscript numbers in parentheses refer to "Literature Cited," page 184.

which show that the first and probably the second of the above conditions prevail, in addition to the fact that the one or two diseased plants in resistant rows occasionally may result from mechanical mixtures.

METHODS AND MATERIALS

Plants were selected from rows showing between 1 and 5 per cent of bunt, with the view of obtaining selections which would breed true for a similar low percentage of bunt. Bunted plants occurring in such rows rarely are completely bunted. Usually such plants will have two or more sound heads, with the result that seeds are available for propagation.

The selections were grown in the field at University Farm, Davis, California. Conditions there favor such investigations, because relatively high bunt infection can be obtained when wheat is sown in the fall. Both spring and winter varieties may be seeded at that time without any danger of winter-killing, and with the assurance that both types will mature in the following summer.

The seeds were thoroughly blackened with bunt by placing an excess quantity of the spores with the wheat in a glass container and shaking vigorously. The inoculum, *Tilletia tritici*, was collected by Professor W. W. Mackie in 1917, on Little Club wheat in the Montezuma Hills district of Solano County, California. This collection was originally propagated by Professor Mackie on Little Club wheat, in the Botany Garden at Berkeley, California. Since 1919 the writer has propagated bunt from this same collection on White Federation wheat at Davis. The inoculum used, therefore, has been derived from one original collection of bunt. This procedure was followed at first, not because it was suspected that there were physiologic forms of bunt, but because this method offered an accessible and definite source of spores. Physiologic forms of this fungus now are known to exist.[5, 6, 7, 8] The fact that the same collection of bunt has been used continuously at Davis makes it reasonably certain that the same form or possibly mixture of forms has been employed in all the writer's investigations. This fact is indicated also by the constant way in which the parental wheat varieties have reacted to this inoculum.

The seeds were spaced from 2 to 3 inches apart in rod rows one foot part. The entire nursery was sown within 3 or 4 days in order to avoid the effects of different temperatures and soil moistures. The nursery always was sown in a field where no wheat had been grown during the previous year, so that it was almost entirely free from volunteer grain.

At harvest time the plants in each row were pulled and separated into two piles: bunt-free and bunted. The total number of plants and the number of bunted plants were recorded and the percentage of infected plants calculated. A plant was classified as bunted if it showed any infection.

The selections all were made from a cross of Hussar with Hard Federation. Hussar is one of the two varieties of wheat found to remain entirely free from bunt when inoculated with spores of *Tilletia tritici* in an extensive test conducted by the Washington, Oregon, and California Agricultural Experiment Stations in cooperation with the Office of Cereal Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture.[9] Hussar has been free from bunt over a 9-year period when inoculated with the bunt collection used in these experiments. It has been attacked by some collections of bunt used elsewhere.[6, 7] Hard Federation is very susceptible to bunt under the conditions of these experiments, as may be seen from the data in table 1.

TABLE 1

ANNUAL PERCENTAGES OF BUNTED PLANTS IN HUSSAR AND HARD FEDERATION WHEATS IN THE 9 YEARS FROM 1920 TO 1928, AT DAVIS, CALIFORNIA

Variety	Percentage of bunted plants									
	1920	1921	1922	1923	1924	1925	1926	1927	1928	9-year average
Hussar	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hard Federation	89.7	62.4	53.3	61.4	82.1	59.8	83.7	84.2	84.6	73.4

There is considerable variation in the percentage of bunted plants in Hard Federation from year to year. Similar fluctuations are exhibited by other varieties, and probably are due to seasonal differences. During the nine years, a total of about 100 rod rows of Hussar and Hard Federation have been grown.

The selections used in these experiments were made from F_4 rows of a cross of Hard Federation with Hussar, made in 1921, for the purpose of studying the inheritance of resistance to bunt. Only the four selections which have been studied most extensively will be considered in this paper. Four rather certain cases of mechanical mixtures occurred in these experiments. It was easy to detect mechanical mixtures because the most extensive plantings were made in F_6 and F_7 and the families therefore were homogeneous for most visible characters. There was a little evidence of field hybridization, but the data are fragmentary and therefore will not be presented.

EXPERIMENTAL RESULTS

The data may be examined to determine whether the occurrence of a few bunted plants in a resistant row is due (*a*) to the fact that genetically resistant plants occasionally may become infected, or (*b*) to the presence of modifying factors.

TABLE 2

PERCENTAGE OF BUNTED PLANTS PRODUCED BY SELECTIONS FROM ROW 478 OF THE F_4 OF HARD FEDERATION x HUSSAR WHEATS

1925 F_4		1926 F_5		1927 F_6		1928 F_7	
Row	Bunted, per cent	Row	Bunted, per cent	Row	Bunted, per cent	Row	Bunted, per cent
				2	0.0	3	0.0
				3	0.0	4	0.0
				4	0.0	5	0.0
				5	0.0	6	0.0
				6	0.0	7	0.0
				7	0.0		
				8	0.0		
				9	0.0	8	0.0
				11	0.0	9	0.0
				12	0.0	10	0.0
				13	0.0	11	0.0
				14	0.0	12	0.0
				15	0.0		
				16	0.0		
		32	0.0	17	0.0		
				18	0.0		
				19	0.0		
				20	0.0	13	0.0
				21	0.0	14	0.0
				22	0.0	15	0.0
				23	0.0	16	0.0
				24	0.0	17	0.0
				25	0.0		
				26	0.0		
				27	0.0		
478 Hard Federation x Hussar	2.8			28	0.0		
				29	0.0		
				30	0.0		
						18	0.0
						19	0.0
				31	0.0	20	0.0
				32	0.0	21	0.0
				33	0.0	22	0.0
				34	0.0		
				35	0.0		
				36	0.0		
				37	0.0		
				38	0.0		
				39	0.0	23*	0.0
				41	0.0	24	0.0
				44	0.0	25	0.0
				45	0.0	26	0.0
				46	0.0	27	0.0
		33*	0.0	47	2.7	28	0.0
				48	0.0	29	0.0
				49	0.0	30	0.0
				50	0.0	31	0.0
				51	0.0	32	0.0
				52	0.0		
				53	0.0		
				54	0.0		
				55	0.0		
				56	0.0		
				57	0.0		
				58	0.0		
				59	0.0		
				60	0.0		

* Row sown from seed of partly bunted plants.

In 1925, row 478 contained one partly bunted plant in a total of 38, or 2.8 per cent of bunted plants. The results obtained by propagating the partly bunted plant and one of the bunt-free plants may be seen in table 2.

In 1927 four rows produced a considerable percentage of bunted plants, but they were so obviously different in morphologic characters that they were discarded as rogues. The good seed produced by the partly bunted plant in 1925 were sown in row 33 in 1926, but no bunted plants resulted. The seeds from 27 plants were sown in 1927. One row contained one partly bunted plant, the seeds from which produced all healthy plants in 1928. The seed from nine sibs likewise gave rise to no diseased plants.

A bunt-free plant selected from row 478 in 1925 and propagated in row 32 in 1926 produced no bunted plants. Forty-three selections of its descendants grown in 1927 and 1928 also were free from bunt.

Certainly, the two rows which produced bunt in the above experiment are nearly, if not quite, as resistant as their sibs. For practical purposes these rows might be considered as resistant genetically as Hussar, even though the one row containing bunt in 1927 was a direct descendant of the partly smutted plant produced in 1925. If the smut appearing in this line is due to modifying factors, the effect is very slight.

Numerous selections have been grown for two or more years without the production of a single bunted head. In fact, the majority of resistant selections obtained from crosses of Martin and Hussar with susceptible varieties resemble the resistant parents in that they never produce any bunt.

If the low percentage of bunt in resistant F_3 rows is due to the action of modifying factors, it should be possible to select lines of wheat which would breed true for this character. A selection was sought which would allow less than 5 per cent of bunt to develop. That such a selection has been obtained may be seen from the data in table 3.

Row 1415 contained one partly bunted plant in 1925. Seeds from this partly smutted plant and from one bunt-free plant were sown and plants grown in the following year. Row 112, from the seed of the partly bunted plant, contained 2.2 per cent of bunted plants in 1926. Row 111, from the seeds of the bunt-free plant, contained no bunted plants. However, in 1927, the progenies from plants of row 112 contained an average of 3.2 per cent of bunted plants. Similar progenies from plants of the bunt-free row 111 contained an average

TABLE 3

PERCENTAGE OF BUNTED PLANTS PRODUCED BY SELECTIONS FROM F_4 ROW 1415 OF HARD FEDERATION X HUSSAR

1925	F_4	1926	F_5	1927	F_6	1928	F_7
Row	Bunted, per cent	Row	Bunted, per cent	Row	Bunted, per cent	Row	Bunted, per cent
1415 Hard Federation x Hussar	3.7	111	0.0	62	1.7	43	0.0
				63	3.8	44	0.0
				64	5.7	45	3.1
				65	2.2	46	0.0
				66	2.9	47	0.0
				67	5.7	48	0.0
				68	3.8	49	0.0
				69	2.0	50	0.0
				70	7.5	51	1.5
				71	0.0	52	0.0
				72	0.0		Av.--0.5
				73	5.9	53*	1.8
				74	0.0	54*	2.4
				75	2.1	55*	1.7
				76	0.0	56	1.7
				77	5.9	57	0.0
				78	0.0	58	0.0
				79	0.0	59	0.0
				80	4.3	60	0.0
				81	15.0	61	2.3
				82	0.0	62	0.0
				83	0.0		Av.--1.0
				84	0.0	33	0.0
				85	6.7	34	0.0
				86	0.0	35	0.0
				87	5.1	36	1.7
				88	1.9	37	0.0
				89	0.0	38	0.0
				90	2.3	39	0.0
					Av.--2.9	40	0.0
						41	0.0
						42	0.0
							Av.--0.2
		112*	2.2	91	8.7	84*	0.0
				92	0.0	85*	1.5
				93	2.3	86	0.0
				94	0.0	87	1.7
				95	0.0	88	0.0
				96	1.6	89	0.0
				97	1.8	90	0.0
				98	3.1	91	0.0
				99	4.9	92	0.0
				100	1.7	93	0.0
				101	5.8		Av.--0.8
				102	3.8	74*	1.6
				103	7.5	75	0.0
				104	11.5	76	0.0
				105	0.0	77	0.0
				106	2.9	78	0.0
				107	0.0	79	0.0
				108	2.6	80	0.0
				109	0.0	81	3.2
				110	0.0	82	1.7
				111	3.3	83	4.0
				112	1.9		Av.--1.1
				113	2.2	63	0.0
				114	0.0	64	0.0
				115	0.0	65	1.5
				116	7.7	66	0.0
				117	4.2	67	0.0
				118	2.8	68	0.0
				119	10.1	69	0.0
				120	4.7	70	0.0
					Av.--3.2	71	0.0
						72	1.9
							Av.--0.3
						94*	0.0
						95*	1.6
						96*	2.1
						97*	0.0
						98*	2.1
						99*	1.9
						100	0.0
						101	0.0
						102	0.0
						103	0.0
						104	0.0
						105	3.4
						106	0.0
						107	2.2
						108	0.0
							Av.--0.9

*Rows planted from the good seeds of partly bunted plants.

of 2.9 per cent of diseased plants. Similar results were obtained in 1928, but the actual percentages of bunted plants were lower.

In 1927, selections were made from bunt-free rows, from rows containing about 2 per cent of bunt, and rows containing near the maximum percentage of bunt produced in that year. In general, selections from rows containing no diseased plants appear to produce a lower average percentage of bunt than selections from rows containing the higher percentages of bunt. Also populations from partly bunted plants usually have a higher average percentage of bunt than populations from bunt-free sibs. However, all the selections from row 111, of 1926, contained an average of 1.15 per cent of bunt in 1927 and 1928, as compared with 1.20 per cent in selections from row 112, which was grown from the seed of a partly bunted plant.

The variation in the percentage of bunt in rows from the same parent was greater in 1927 than in 1928. This suggests that these differences probably are due to environmental influences. The fact that rows containing the higher percentages of bunt in 1927 usually produced progeny having slightly higher percentages in 1928 might indicate that a greater number of modifying factors are present in these rows, or possibly that factors with a greater effect are involved. Because of environmental influences it is impossible to get an exact expression of the influences of these factors, and therefore it is undersirable to draw too fine distinctions.

That the effects of modifying factors may be considerably greater than those just considered may be seen from the data in table 4.

In 1925 row 1417 contained one partly bunted plant. Plants from the seeds of this partly bunted plant and from one bunt-free plant were grown in 1926, and their progenies in 1927. The partly bunted selection (row 117) gave rise to lines very similar to those shown in table 3. However, the bunt-free selection (row 116) produced one partly bunted plant out of a total of 21, or 4.8 per cent. Plants from the seeds of this partly bunted plant, together with those from 16 bunt-free plants, were grown in 1927. The row (No. 152) from the seeds of the partly bunted plant contained 40 per cent of bunted plants. The rows from the bunt-free plants produced from 0 to 25 per cent of bunt in 1927. Selections from row 165, with no bunt, and row 158, with 1.9 per cent of bunt, produced lines in 1926 similar to those already considered in table 3.

Selections from row 156, which contained 22.9 per cent of bunted plants, produced an average of 5.1 per cent of diseased plants in 1928. The 22.9 per cent of bunted plants in row 156 at first suggested that it must have resulted from a natural cross with some susceptible plant

TABLE 4

PERCENTAGE OF BUNTED PLANTS PRODUCED BY SELECTIONS FROM F_4 ROW 1417 OF HARD FEDERATION X HUSSAR

1925 F_4		1926 F_5		1927 F_6		1928 F_7	
Row	Bunted, per cent	Row	Bunted, per cent	Row	Bunted, per cent	Row	Bunted, per cent
1417 Hard Federation x Hussar	4.0	116	4.8	152*	40.0	129*	12.0
						130*	0.0
						131*	1.4
						132*	3.3
						133*	3.3
						134*	10.0
						135*	5.2
						136*	10.8
						137*	18.9
						138*	7.3
						139*	1.5
						140*	7.4
				153	9.9	141	1.7
				154	25.0	142	1.5
				155	9.5	143	0.0
				156	22.9	144	0.0
				157	11.1	145	1.6
				158	1.9	146	2.6
				159	20.0	147	0.0
				160	16.9	148	13.0
							Av.--5.1
				161	1.6	119	0.0
				162	5.0	120	0.0
				163	8.7	121	0.0
				164	18.5	122	0.0
				165	0.0	123	0.0
				166	12.5	124	3.6
				167	14.2	125	0.0
				168	8.3	126	1.7
					Av.--13.3	127	0.0
						128	0.0
							Av.--0.5
						109	0.0
						110	1.8
						111	0.0
						112	0.0
						113	1.6
						114	0.0
						115	0.0
						116	3.5
						117	0.0
						118	0.0
							Av.--0.7
						170*	0.0
						171*	0.0
				169*	3.3	172	0.0
				170	2.6	173	0.0
				171	6.2	174	0.0
				172	0.0	175	0.0
				173	3.3	176	0.0
				174	3.0	177	0.0
				175	7.1	178	0.0
				176	0.0	179	0.0
				177	0.0		Av.--0.0
				178	7.7	150	0.0
				179	4.2	151	0.0
				180	1.6	152	0.0
				181	0.0	153	0.0
				182	0.0	154	0.0
				183	6.7	155	1.8
		117*	2.1	184	7.9	156	0.0
				185	0.0	157	1.5
				186	2.7	158	0.0
				187	1.8	159	0.0
				188	0.0		Av.--0.3
				189	13.0	160	1.6
				190	3.6	161	3.4
				191	14.8	162	1.5
				192	0.0	163	1.8
				193	1.8	164	0.0
				194	0.0	165	0.0
				195	1.6	166	0.0
				196	0.0	167	0.0
				197	2.1	168	0.0
				198	0.0	169	0.0
					Av.--3.2		Av.--0.8
						180*	3.6
						181*	0.0
						182*	1.6
						183*	1.6
						184*	1.3
						185	0.0
						186	0.0
						187	3.3
						188	3.0
						189	0.0
						190	0.0
						191	8.1
						192	1.6
						193	0.0
						194	Av.--1.7

*Row planted from the good seeds of partly bunted plants.

and was heterozygous for resistance. However, it differed in one important respect from heterozygous rows previously observed. In heterozygous rows resulting from a cross between a susceptible and a resistant wheat from a third to a half or more of the diseased plants are completely bunted, and consequently produce no seed. On the other hand, all the diseased plants in row 156 were only partly bunted, and seeds from them were used for growing plants in 1928. In fact, almost without exception the diseased plants in all the selections in these experiments were partly bunted. That row 156 did not come from a heterozygous plant will be seen from the results obtained in 1928. Because considerably more bunt was produced in this family than in any of the other families, the results suggest that probably a larger number of modifying factors are present, or perhaps that the modifying factors present exert a greater effect.

DISCUSSION AND CONCLUSION

It is beyond the scope of this paper to review or discuss in any detail the literature dealing with modifying factors. The effects of modifying factors are frequently met with in genetical experiments, and they have been referred to on numerous occasions in the literature.

Serious attention first was attracted to modifying factors by the controversy in genetic circles arising over the belief that the hooded factor in rats was very unstable. Starting with a common foundation stock, Castle,[3] by selecting in the minus direction, practically eliminated the colored areas, whereas in the plus direction he produced a race which was almost self-colored. As Castle had previously found that hooded pattern differed from self-color in a single recessive factor, he believed that the selection experiments showed that selection had altered the hooded factor. The adherents to the multiple-factor hypothesis, on the other hand, held that the hooded factor simply is necessary for the development of the hooded pattern, but that the degree of pigmentation may be modified by numerous other factors. Castle[4] himself eventually demonstrated the correctness of the multiple-factor hypothesis.

In general, the effects of modifying factors are seen most frequently in connection with quantitive characters. In such material it is difficult to distinguish clearly between the actions of these factors and the effects of environment. Consequently, the study of modifying factors has been an unattractive field. In practically all cases nothing definite is known about them beyond the fact that they do exist.

Bridges[1] seems to have reported the only extensive study of modifying factors. In *Drosophila* studies he found eight specific modifiers of eosin eye color. He not only demonstrated the existence of modifying factors for eosin eye color, but also studied them individually, showing that they differ in no essential respects from other factors. Also he located some of them on the chromosome map.

The data presented in this paper demonstrate the presence of factors which modify the resistance of wheat to bunt. This information should make possible a more complete understanding of the results obtained when a bunt-resistant wheat is crossed with a susceptible one. The occurrence of a low percentage of bunt in resistant F_3 rows is explained adequately. Furthermore, these data suggest a possible explanation for a part of the variability met with in rows of other genotypes. Heterozygous and homozygous susceptible F_3 rows vary considerably in the percentage of bunt which they contain. No doubt a considerable amount of this variation is due to environmental influences. However, it is reasonable to suppose that a part of it may be due to modifying factors.

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